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Growth and Cone Production of Knobcone Pine Under Interrupted Nights

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ABSTRACT: Four-year-old knobcone pines (*P. attenuata* Lemm.) from 11 sources were illuminated for 1 hour at midnight from either March 21 to June 21, or June 22 to Sept. 21 at the Institute of Forest Genetics, Placerville, California. The light treatments had no effect on the number of trees flowering during the next year, on height growth or its seasonal distribution, or on the frequency of summer shoots. Seed source strongly influenced flower production, height growth, and seasonal distribution of height growth. A rapidly growing one-parent progeny owed much of its superiority to a surge of growth in late summer. The morphology and development of these trees was observed.

Many recent experiments have shown that long photoperiods may stimulate height growth of conifers (for example: Fraser 1962; Fowler 1961; Kramer 1957; McGregor et al. 1961; Watt 1961). The same result has been obtained by interrupting the night with a short period of light (Downs and Piringer 1958; Zahner 1955; Zelawski 1957). Interrupting the dark period converts phytochrome pigment back to the far-red absorbing form, permitting growth to continue (Downs 1962). The additional height growth may be due to an increased number of growth flushes (McGregor et al. 1961; Watt 1961; Watt and McGregor 1963), a longer growing period (Kramer 1957; Olson and Nienstaedt 1957; Zahner 1955), or a combination of both (Downs and Piringer 1958).

The effect of photoperiod on cone production of pines has received less study (Nienstaedt 1961). Mirov (1956) has presented evidence that suggests pines are neither short-day nor long-day plants. Holst (1959) has reported that cone production of 4-year-old potted stock of red pine (P. resinosa Ait.) was not affected by exposure to short days. However, Wareing and Longman (1960) and Longman (1961) found that long days increased the production of cones of both sexes on Scotch pine (P. sylvestris L.), and short days stimulated female cone production in lodgepole pine (P. contorta Dougl.).

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[1] Both the lighting regime and the idea of applying it to trees approaching the reproductive stage were originally conceived by Dr. N. T. Mirov. I am grateful to C. M. Blankensop for field assistance and to Mrs. R. R. Taylor for much of the statistical analyses.

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In 1961 saplings of knobcone pine (Pinus attenuata Lemm.) were exposed to interrupted-night treatments to study their response in height growth and cone production. This paper reports on the results of that study.

METHODS

Knobcone pine is a closed-cone pine found in scattered groves from northern Baja California, along the Coast Range and Sierra Nevada foothills of California, to southern Oregon.

The trees under study represented 11 sources (table 1 and fig. 1). All were from seed collected in 1957 and sown in nursery beds the following spring at the Institute of Forest Genetics, Placerville, California. When the experiment was begun in March 1961, they were entering the fourth growing season. Four trees of each source received the following treatments:

Control:	Natural day and night.
Spring long-day:	Night interrupted from midnight to 1 a.m., March 21 to June 21.
Summer long-day:	Night interrupted from midnight to 1 a.m., June 22 to September 21.

Table 1. --Knobcone pine seed sources

California county	Plot and tree no.[1]	Latitude	Longitude	Elevation (feet)
Santa Cruz	2-Mix	37° 03'	122° 08'	1,800
Napa	1-Mix	38° 39'	122° 37'	3,800
Lake	1-5	38° 54'	122° 47'	2,600
Lake	3-Mix	39° 15'	122° 48'	2,350
Humboldt	1-Mix	41° 05'	123° 36'	3,500
Siskiyou	4-1	41° 44'	123° 01'	1,600
Mariposa	1-Mix	37° 32'	119° 59'	3,000
Eldorado	4-Mix	38° 59'	120° 42'	3,200
Placer	1-Mix	39° 01'	120° 49'	3,200
Placer	2-Mix	39° 10'	120° 52'	3,200
Nevada	1-Mix	39° 22'	120° 57'	3,000

[1] "Mix" seed is collected from several trees at the location.

Light was provided by incandescent lamps suspended above the trees and operated by an automatic timer. At 3 feet above the ground light intensity varied from 26 to 140 foot-candles. Light-proof screens confined the light to the nursery beds in which the treated trees were grown. Similar screens were erected around the unlit control bed in

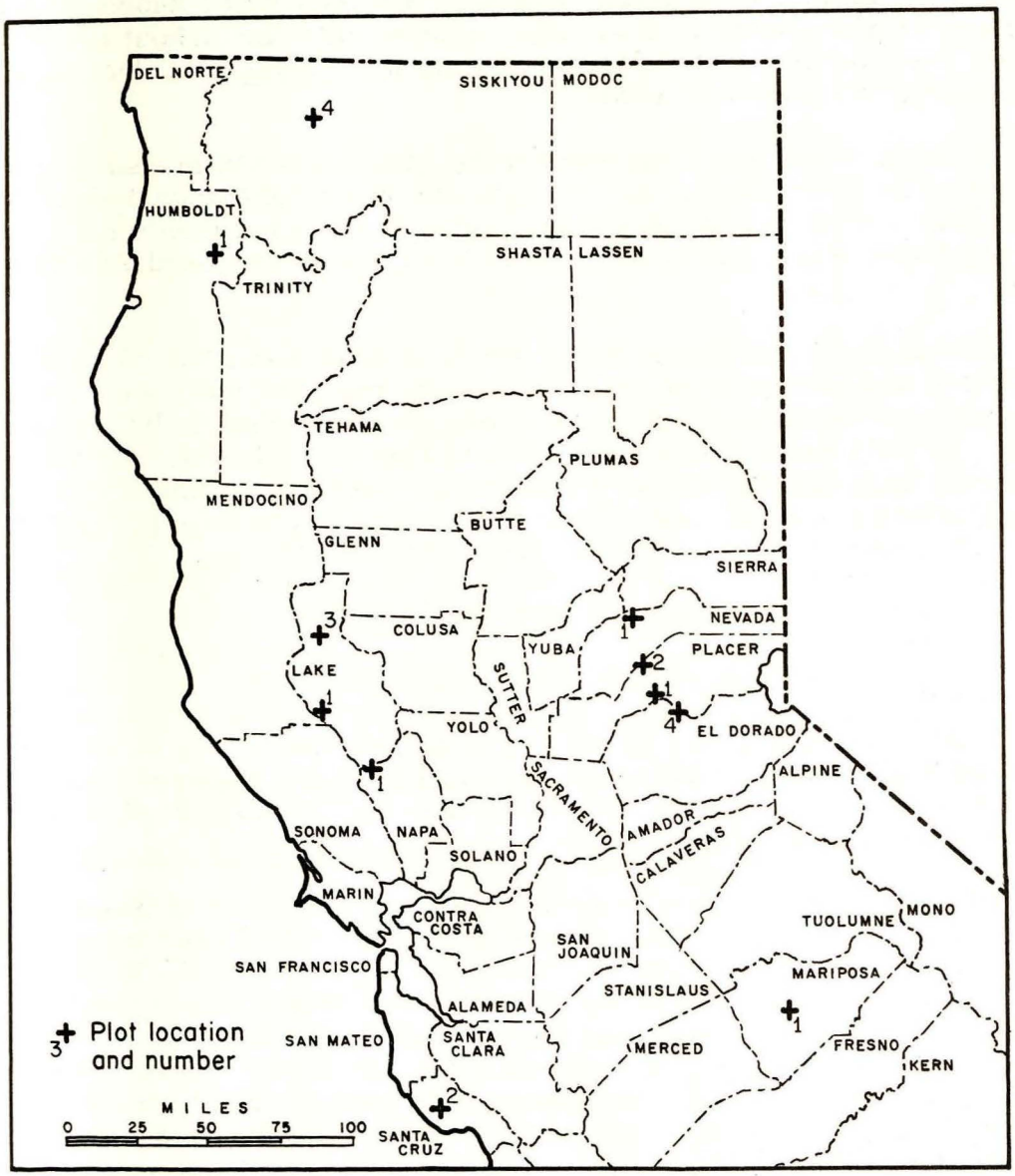

Figure 1. --Location of knobcone pine seed sources.
(See also Table 1.)

order to insure uniformity in shading of all treatments. While the lights were on, no light could be detected in the control bed, it being even too dark to read a light meter.

Weekly height measurements were made from a pin inserted in the previous year's terminal to the tip of the leading bud or shoot. When the first measurement was made, on March 28, buds had just started to elongate in trees from almost all sources. However, this date was arbitrarily considered the first day of the growing season, and December 12 the last day. Therefore, the season's growth is understood to mean

growth from March 28 to December 12. Actually some knobcone pines continued height growth at a greatly reduced rate throughout the year, as does the closely related Monterey pine (P. radiata D. Don) (Anonymous 1953; Shreve 1924).

Several trees were excluded from height-growth measurements because of damaged leaders. In analyzing the height-growth data only three trees per source finally were included for each treatment. When only two trees were left for analysis, their mean was used as a third value.

Cones were counted in early April of 1961 and 1962. By then pollination had occurred or was imminent, and both male and female cones were conspicuous. Female cones were counted individually both years. In 1961 male cones were also tallied individually, but in 1962 this would have been too time-consuming. Instead I counted the number of axes bearing male cones. Thus the change in absolute production of male cones cannot be ascertained from these data.

RESULTS AND DISCUSSION

CONE PRODUCTION

Only a few trees had borne cones before 1961. All those that produced male cones in 1961 and survived until the next year also produced some in 1962. Of the five trees bearing female cones in 1961, four did likewise in 1962.

Photoperiod treatments did not affect the number of trees producing cones of either sex. The control group did have fewer trees with male cones in 1962 than either of the treated groups (table 2), but this difference is probably due to the loss of three trees before the 1962 cone count. All three trees had borne male cones in 1961. Had they survived and produced male cones in 1962, as seems likely, 40.4 percent of the controls would have borne male cones. This result compares closely with 43.6 and 42.5 percent for spring long-day and summer long-day treatments (table 2).

Applying the same correction to percent of trees bearing female cones (table 3) would increase cone production on spring long-day trees to 15.0 percent. This differs little from 16.2 and 17.5 percent for the controls and the summer long-day trees.

In 1961 some trees from 6 of the 11 sources produced male cones and trees of 4 sources produced female cones. In 1962 trees of only one source--Siskiyou 4-1--failed to produce male cones, and trees of four sources--including Siskiyou 4-1--failed to bear female cones. In 1962 trees of the one-parent progeny Lake 1-5 bore 27 of the 43 cones produced (63 percent). This is interesting because as will be shown below, the progenies Lake 1-5 and Siskiyou 4-1 were the most and least vigorous of the 11 in terms of vegetative growth as well as reproductive capacity.

Table 2. --Percent of trees bearing male cones, by treatment and source

Source	Control		Spring long-day		Summer long-day		Source means	
	1961	1962	1961	1962	1961	1962	1961	1962
Santa Cruz 2-Mix	0	25	0	25	0	33	0	27
Napa 1-Mix	0	100	25	67	25	100	16	88
Lake 1-5	[1/] 75	100	50	100	67	100	64	100
Lake 3-Mix	0	0	50	100	0	0	16	30
Humboldt 1-Mix	25	50	0	0	0	0	8	16
Siskiyou 4-1	0	0	0	0	0	0	0	0
Mariposa 1-Mix	0	0	0	75	0	0	0	25
Eldorado 4-Mix	[2/] 25	0	0	50	25	50	16	40
Placer 1-Mix	75	100	0	0	25	75	33	60
Placer 2-Mix	0	25	0	33	0	50	0	36
Nevada 1-Mix	0	0	0	33	0	75	0	40
Treatment Totals	18.2	32.4	11.4	43.6	11.6	42.5	13.7	37.1

[1] Two trees that flowered in 1961 died before the 1962 count.
[2] The single tree that flowered in 1961 died before the 1962 count.

Table 3. --Percent of trees bearing female cones, by treatment and source

Source	Control		Spring long-day		Summer long-day		Source means	
	1961	1962	1961	1962	1961	1962	1961	1962
Santa Cruz 2-Mix	0	0	0	0	0	0	0	0
Napa 1-Mix	0	0	25	0	0	33	8	11
Lake 1-5	0	50	25	50	0	100	9	78
Lake 3-Mix	0	0	[1/] 25	67	0	0	8	20
Humboldt 1-Mix	0	0	0	0	0	0	0	0
Siskiyou 4-1	0	0	0	0	0	0	0	0
Mariposa 1-Mix	0	0	0	0	0	0	0	0
Eldorado 4-Mix	0	0	0	0	0	25	0	10
Placer 1-Mix	50	67	0	0	0	50	16	40
Placer 2-Mix	0	25	0	0	0	0	0	9
Nevada 1-Mix	0	33	0	33	0	0	0	20
Treatment Totals	4.5	16.2	6.8	12.8	0	17.5	3.8	15.5

[1] The single tree that flowered in 1961 died before the 1962 count.

HEIGHT GROWTH

Neither spring long-days nor summer long-days influenced growth during the spring, summer, or entire growing season. And neither of the long-day treatments affected the percent of season's growth accumulated at any of the 29 observation times (fig. 2). These findings are based on analyses of variance of source means by which the two long-day treatments were compared with the control. No differences were significant at the 5 percent level.

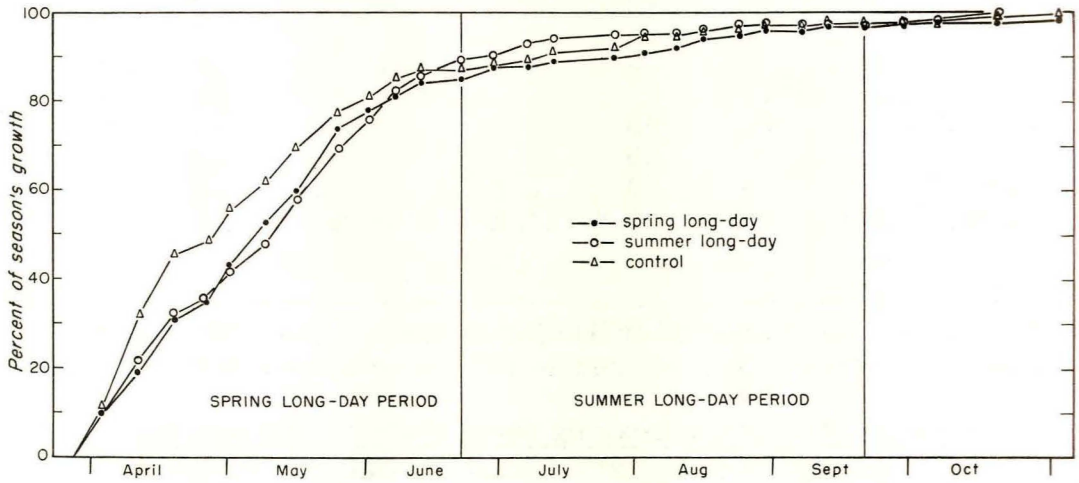

Figure 2. --Mean cumulative growth curves of trees grouped by light treatment. During late April and early May the controls differed significantly from the other treatments; but during this period the summer long-day group was, in effect, a control group, for it was not illuminated until June 22.

Within each of the 11 sources, growth was unaffected by the long-day treatments. Analyses of variance showed no significant differences (5 percent level) due to treatment in total season's growth, or growth during either of the long-day periods.

Summer or lammas shoots were commonly observed, but their occurrence was not related to the long-day treatments (table 4). Most of these shoots could still be identified the following spring by their short needles. The earliest summer-shoot flush was observed on May 25, the latest on August 24.

Interrupting the dark period, whether early or late in the growing season, clearly did not affect either amount or distribution of growth. The long-day treatments also failed to lengthen or shorten the growth period or influence the frequency of summer-shoots.

These results are at variance with those of most other workers, for typically, increased daylength has increased height growth. The

design of the experiment does not appear to be a factor in causing the lack of response. In other experiments, a light break of half an hour has been enough to elicit a response, as have lesser light intensities. Although it is impossible to establish ex post facto the reason these knobcone pines did not react to the light treatment, it is worthwhile to consider certain possibilities.

Table 4. --Seasonal occurrence of summer (lammas) shoots among treatments

Treatment	Trees with summer shoots as fraction of trees in group		
	In spring	In summer	Total
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Control	5/37	4/37	9/37
Spring long-day	10/39	5/39	15/39
Summer long-day[1]	9/40	9/40	18/40
Total	24/116	18/116	42/116

[1]During the spring the summer long-day group was, in effect, a control group.

Vaartaja (1959) found that when seedlings of several pines (and many other genera) were exposed to a variety of daylength regimes, he could discern for each a "critical daylength," that is, the longest daylength at which height growth was inhibited. For example, Scotch pine from latitude 60° N. showed growth inhibition under daylengths equivalent to 12, 14, and 16 hours, but not under 18 hours. Its critical daylength is therefore 16 hours. For pines of more southerly origin, where natural daylength is shorter, the critical daylength becomes progressively shorter. According to Vaartaja's (1959) data, the critical daylengths for eastern white pine (P. strobus, L.), red pine, and pitch pine (P. rigida Mill.) are all about 12 hours. The latitudes of origin were 43° N. for red pine and 35° N. for the other two species. The knobcone pine in the tests reported here originated between 37° and 42° N. latitude (table 1), and in light of Vaartaja's work it is reasonable to expect knobcone pine to be relatively unaffected by succeeding increments of light beyond 12 hours. In this experiment all of the trees--including the controls--were exposed to maximum daylengths of at least 15 hours, and the long-day treatments gave a maximum daylength equivalent of about 21 hours.

The critical daylength concept appears applicable to other cases in the literature. In ponderosa pine (P. ponderosa Laws.), for example, Callaham (1962) found comparatively little difference in height growth between seedlings under 8-hour days and those under 12-hour days. However, increasing the daylength to 16 hours brought about a fourfold growth response in some sources.

Vaartaja (1959) failed to elicit any growth differences in Monterey pine seedlings exposed to his range of daylength treatments. He regarded this as "truly exceptional", but perhaps it merely signifies that Monterey pine has a critical daylength of less than 12 hours, the shortest daylength Vaartaja used. Both phylogenetically and geographically knobcone and Monterey pines are close neighbors (they hybridize occasionally where their natural ranges overlap). So one possible explanation of the present experiment's results is that even the natural days exceeded the critical daylength for knobcone pine.

A second possibility suggests itself from Vaartaja's comment, quoted above. It may be that both knobcone and Monterey pines are insensitive to changes in length of day.

Another possibility that could explain the results of this experiment, but not Vaartaja's results with Monterey pine, is that the knobcone pines were beyond the age at which daylength sensitivity is evident. The great bulk of photoperiod study of trees has been done with first-year and second-year seedlings; but when older trees were used negative results have sometimes been obtained. Watt (1961), for example, reported increased height growth of eastern white pine and red pine when they were exposed to 20-hour photoperiods during their first and second years. But during the third and fourth years both species "had increasingly smaller percentages of plants making a second flush of growth so that during the fourth year the shape(s) of the growth curves... were the same under long and short day."[2] Each growth curve was based on 60 trees.

Quite similar results have been obtained by Goddard[3] with seedlings and grafts of slash pine. During the first year of his study, when the seedlings and grafts were 3 years old, both interrupted nights and continuous lighting (24-hour days) greatly stimulated height growth. But during the second year of treatment, little difference in growth was evident among treatments. Therefore, the lack of response of the knobcone pines could be a function of the age of the trees; they were 4 years old and many were already flowering. The question of age and its relationship to photoperiod response is not at all clear and warrants further study.

It is notable that in some experiments in which the results are purported to have shown growth increases due to long days, the experimental conditions were such that they may really have only demonstrated the inhibitory effects of abnormally short days. The long-day treatment used by Zahner (1955) had a day length equivalent of over 17 hours (assuming the interruption of darkness negates all of the previous dark period). But his control had only 9.5 hours of light per day--hardly longer than midwinter days at that latitude. McGregor et al. (1961) used long-days of 15 hours, but their short days were also 9.5 hours, and their work was at the same location as Zahner's.

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[2]Personal correspondence with Richard F. Watt, Sept. 25, 1962.

[3]Personal correspondence with Ray E. Goddard, June 15, 1962 and May 13, 1963.

Effect of seed source

Analyses of variance supplemented by Duncan multiple range tests show that seed source strongly influenced height growth. In terms of total season's growth, trees from Lake 1-5 grew significantly more (5 percent level) than all others, and trees from Siskiyou 4-1 significantly less than all others. Growth during the early and late parts of the season differed slightly in detail (table 5), but the trees from Lake 1-5 were always the most vigorous, those from Siskiyou 4-1 the least vigorous.

The annual growth superiority of trees from Lake 1-5 and the inferiority of those from Siskiyou 4-1 were not unexpected. After 4 years in the nursery, these trees averaged about 7.5 and 3.0 ft. tall; trees from the other nine sources ranged from 4.5 to 5.5 ft. It is interesting, however, that growth in Lake 1-5 deviated from the others not in the early part of the season, but after June 22. This will be discussed in greater detail below.

Regressions on latitude and elevation of seed source were made with the following attributes: (a) number of days between attainment of 10 and 90 percent of total growth; (b) total growth; (c) growth from March 28 to June 21; (d) growth from June 22 to Dec. 12; and (e) date at which 50 percent of total growth was attained. Each of these regressions was nonsignificant; they showed no evidence of a continuous geographic pattern of variation. This cannot be taken as evidence that clinal patterns are absent, however, because these sources represent only 4° 31' of the approximately 10° latitudinal range of knobcone pine.

Variation within one-parent progenies

Siskiyou 4-1 and Lake 1-5 are both from single-tree seed collections, and are useful in demonstrating variation in growth rhythm within a one-parent progeny.

The individual tree curves of the progeny Siskiyou 4-1 are quite similar in shape (fig. 3A). The grand period of growth occurred during April and May, and a second growth surge in several trees was caused by extension of summer-shoots in mid-June. One tree which was heavily shaded by a light-proof screen started growth at a very slow rate in 1961. In 1962, after the screen had been removed, its growth was found to be similar to that of its neighbors. This effect of shade delaying the onset of growth, has also been observed by Baldwin (1931).

The progeny Lake 1-5 tended towards a bi-modal pattern of height growth (fig. 3B). The most extreme example was a tree that had attained only 53 percent of its total growth by June 21. It is instructive to compare this tree with one from source Lake 3-Mix, geographically a close neighbor. To June 21 the bi-modal tree had grown 489 mm. and the more conventional one had grown 466 mm. By Dec. 12, the total growth figures were 919 and 564 mm. Thus the superior growth of this tree of Lake 1-5 was largely due to the magnitude of its second growth surge during late summer and fall. This study was conducted in the third year of a severe drought, the rainfall from May 12 to Nov. 20 totaling less than

Table 5. --Total season's growth, early growth, and late growth in knobcone pine, by seed source

Total season's growth Mar. 28 - Dec. 12			Early growth Mar. 28 - June 21			Late growth June 22 - Dec. 12		
Source	Mean growth	Stat. sig.[1]	Source	Mean growth	Stat. sig.[1]	Source	Mean growth	Stat. sig.[1]
	Mm.			Mm.			Mm.	
Lake 1-5	718		Lake 1-5	487		Lake 1-5	230	
Humboldt 1-Mix	545		Eldorado 4-Mix	432		Humboldt 1-Mix	118	
Eldorado 4-Mix	509		Humboldt 1-Mix	426		Mariposa 1-Mix	111	
Napa 1-Mix	505		Santa Cruz 2-Mix	415		Napa 1-Mix	103	
Mariposa 1-Mix	505		Lake 3-Mix	409		Eldorado 4-Mix	77	
Santa Cruz 2-Mix	481		Napa 1-Mix	402		Santa Cruz 2-Mix	66	
Lake 3-Mix	453		Placer 2-Mix	402		Nevada 1-Mix	65	
Placer 2-Mix	449		Mariposa 1-Mix	394		Placer 1-Mix	53	
Nevada 1-Mix	446		Placer 1-Mix	393		Placer 2-Mix	47	
Placer 1-Mix	446		Nevada 1-Mix	381		Lake 3-Mix	44	
Siskiyou 4-1	273		Siskiyou 4-1	241		Siskiyou 4-1	32	

[1] Statistical significance (5 percent level). Mean separation by Duncan multiple range test.

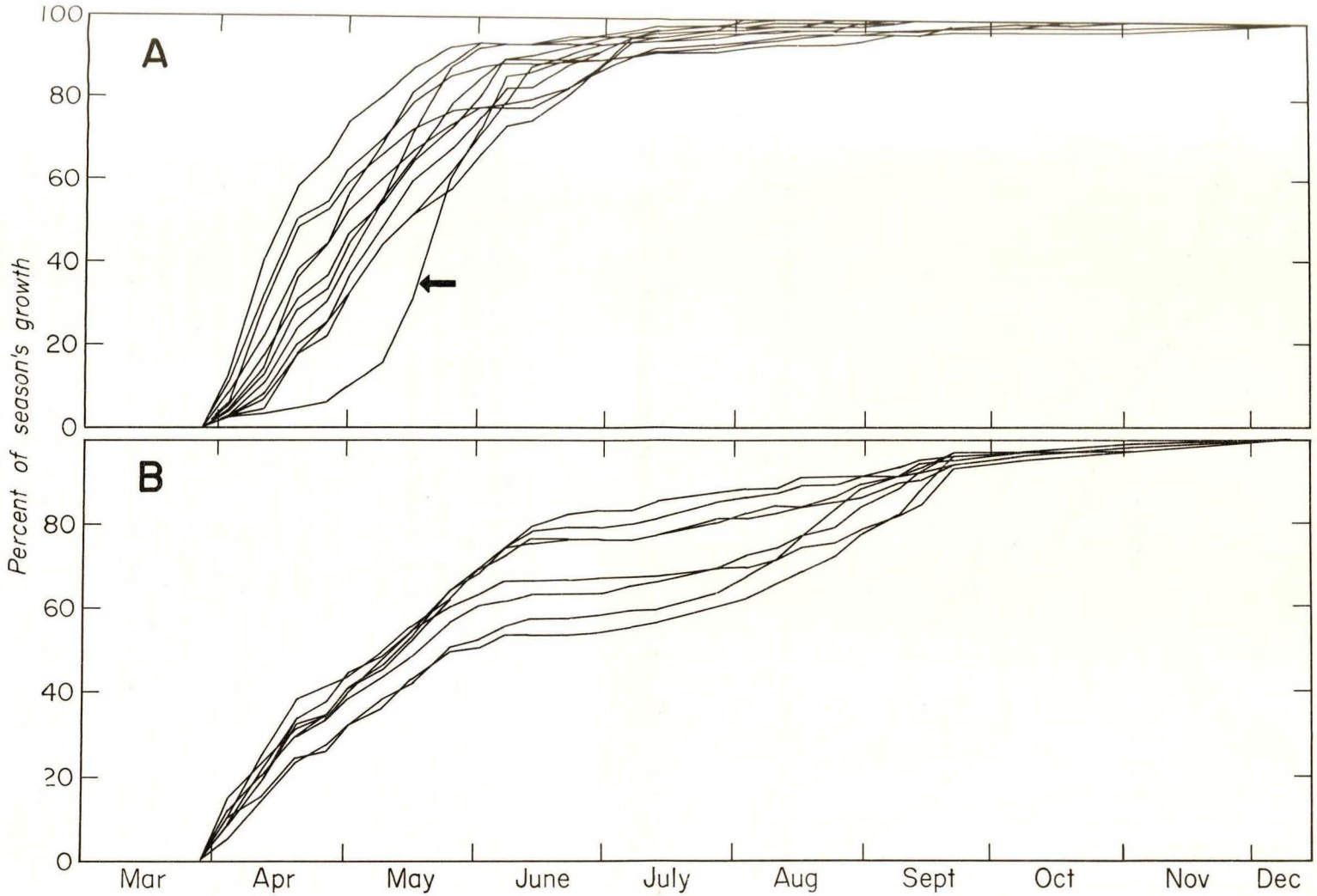

Figure 3. --Cumulative growth curves of trees from 2 one-parent progenies. (A) Siskiyou 4-1; (B) Lake 1-5. The tree in 3A indicated by arrow was heavily shaded.

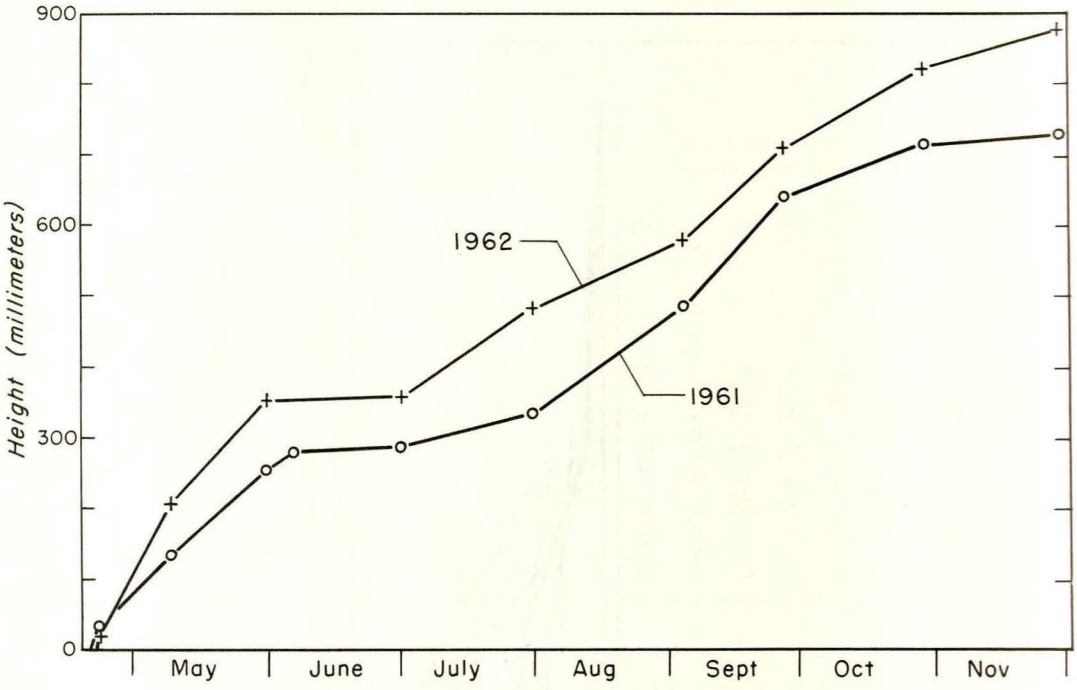

Figure 4. -- Bi-modal growth pattern of a tree of source Lake 1-5 during 1961 and 1962. This tree had shoots morphologically similar to those shown in Fig. 5.

1 inch. Therefore, the bi-modal growth pattern cannot be attributed to replenishment of soil moisture. Observations made in 1962 show a striking similarity of the growth curves for 1961 and 1962 in the tree discussed above (fig. 4). Other trees that were bi-modal in 1961 were also bi-modal the following year.

The bi-modality of these shoots was not the result of a typical "second flush" in which the newly-formed winter bud opened and was superseded by a new bud at the shoot apex. In these trees the winter bud formed in June and the second growth surge resulted from extension at the base of the bud while the major portion of the bud remained intact. In some trees this elongation of the basal part of the bud exposed only the sterile-bract area; in other trees up to 25 or 30 cm. (10 or 12 inches) of the fascicle-bearing region also was exposed.

This late-forming section of shoot was easily identified even in the spring after its development. The fascicle buds remained dormant while the shoot hardened off and turned nut-brown, the condition in which it overwintered. The next spring, when the newly-extended internode above was making rapid growth, the fascicle buds on the bare

Figure 5.--Typical shoot system of a knobcone pine with bi-modal growth habit, April 22, 1962. The lower portion of the stem elongated during the spring of 1961. It bears needles of normal length. The internode just above this elongated in late summer and fall 1961; this is termed the "bare overwintering shoot" in the text. Its needles are just penetrating the sheaths. The long internode above this and the short one at the tip result from elongation in April 1962. Here, too, needles are just emerging.

overwintering shoot underwent their normal development. These fascicles (or in some cases, male cones) developed at about the same time as those on the new shoot (fig. 5). This pattern of shoot growth, characterized by the premature elongation of the bud, which was then arrested until spring, was in contrast to the normal pattern in Pinus (Sacher 1954; Tepper 1963). Also, it bore little in common with the "multiphase growth" of southern pines (Eggler 1961).

Observations of many more knobcone pines of various provenances show that the bi-modal growth pattern is not uncommon in this species, though it is not usually as pronounced as in the source Lake 1-5.

Further investigation of this type of growth is in progress.

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